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Stress reaction in freshwater fish in response to extreme impacts and during the reproduction period

Vladimir Ivamovich Martemyanov*

Papanin Institute for the Biology of Inland Waters, Russian Academy of Sciences, 152742 Borok, Yaroslavl oblast, Russia

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ABSTRACT

The original and published data on the physiological and biochemical reactions in fish in response to stress impact and during the reproduction period are presented. It is shown that at the initial period of stress and before spawning the protective functions in fish are enhanced which relates to the adaptation syndrome. However, during the initial period of stress the damaging effects prevail over the adaptive processes resulting in the decrease in the level of resistance ("alarm reaction" according to Selye). In contrary, during pre-spawning period protective systems dominate along with enhancement of general adaptation syndromes. This facilitates the increase in the level of resistance in the parental fish ("resistance stage" according to Selye). Before the spawning the alarm stage is not manifested. The state comparable to strong stress occurs in the parental fish only during the spawning. This state is accompanied by decrease in the resistance of organism in spawner evidencing exhaustion of protective functions ("exhaustion stage" according to Selye). With time, both at stress and after spawning, within two to three weeks period, the physiological-biochemical parameters recover and stabilize with the normal limits.

1. Introduction

Several researchers have noted that during the reproduction period parental fish exhibit the state resembling stress[1-4]. It is unclear if the stress in reproducing fish identical to the stress in response to extreme factors or are there any differences between these states? Clarification of this uncertainty necessitate the comparative analysis of physiological and biochemical processes observed in fish in response to stressors and during the period of reproduction.

*Corresponding author: Vladimir Ivamovich Martemyanov, Papanin Institute for the Biology of Inland Waters, Russian Academy of Sciences, 152742 Borok, Yaroslavl oblast, Russia.

E-mail: martem@ibiw.yaroslavl.ru

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2. Dynamics of physiological and biochemical parameters in freshwater fish from the beginning of stress impact to the end of acclimation to new conditions

The comparative analysis of available data revealed the consequence of the processes taking place in freshwater fish in response to stress impacts[5]. It was shown that on the one hand the stressors cause a series of damages in the organism (Figure 1, right part), but on the other hand, enhance the protective functions (Figure 1, left part) withstanding development of harmful processes.

2.1. Damaging effects of stress-factors

Many factors of physical and chemical (toxicants) natures cause direct structural damages, first of fish gills[6]. However, all types of

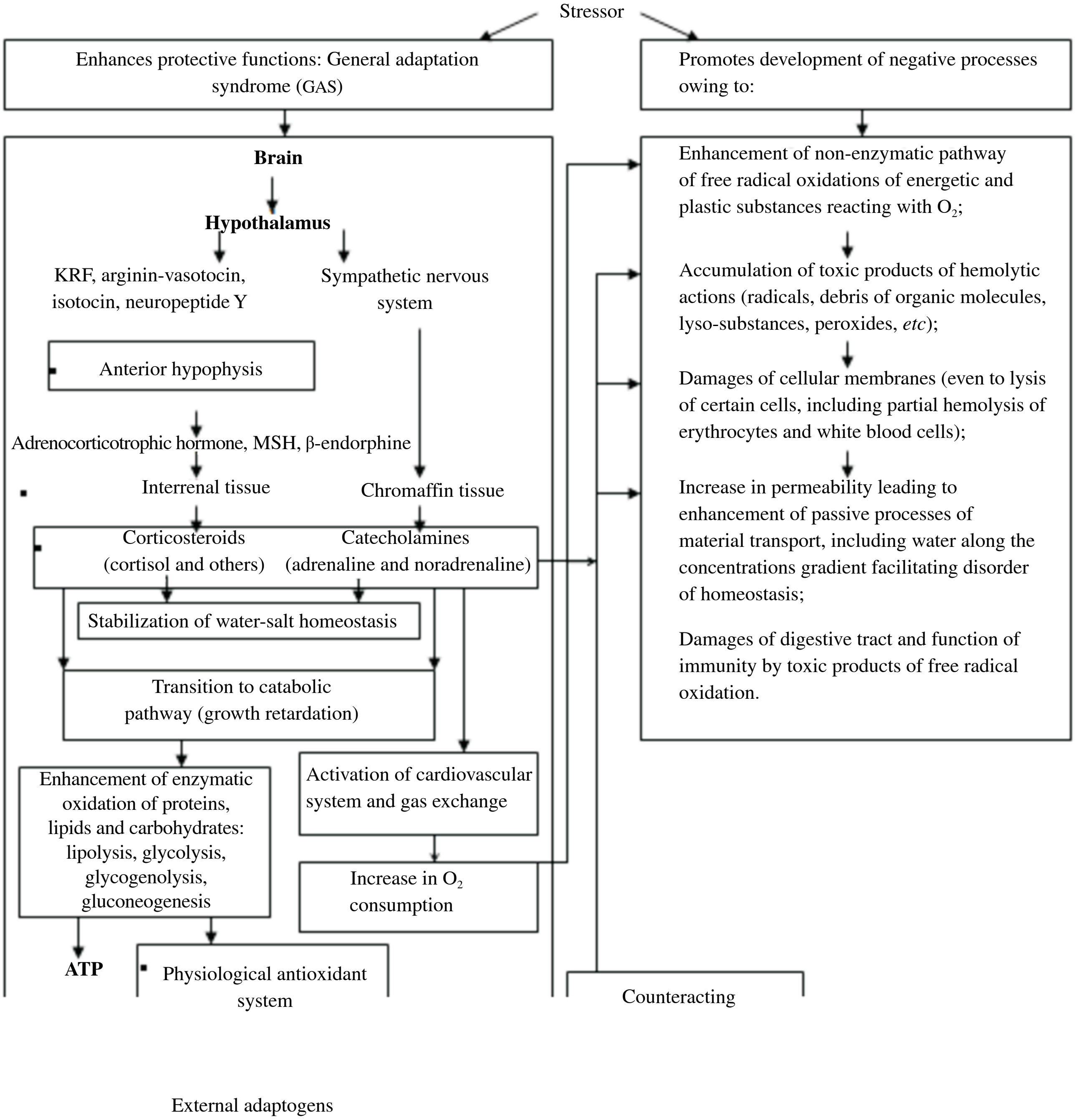

Figure 1. Schematic diagram of the conjugated processes related to the GAS (left part) and negative symptoms (right part) during the stress[5]. MSH: melanophor-stimulating hormone.

stressors possess common mechanism of destabilization of organism. In 1972 it was hypothesized that damaging and malfunctions at stress are realized via peroxides and free radicals[7]. The stressors reinforce nonenzymatic pathway of the oxidation by free radicals of energetic and plastic substances in the organs and tissues[8]. This results in the formation of aggressive free radicals. These radicals directly bind with oxygen and produce toxic peroxidation products.

It was shown that during initial stage of stress the organs and tissues of mammals[7,9,10], and fish[11-15] accumulate harmful substances possessing hemolytic activity: aggressive radical, "debris of organic molecules, lipid peroxides, *etc*. These substances cause various damaged in the organism (Figure 1, right part), including increase in the permeability of cellular membranes. As a result, the blood passing fish gill capillary system loses ions, mainly sodium and chlorine[16-21]moving into the freshwater. This leads to the decrease in concentration of these electrolytes in the organism's internal environment[16-18,20,22] (Figure 2).

Decline of the level of sodium and chlorine ions in the blood plasma of freshwater fish that takes place during the initial stage of stress is accompanied by drop of the osmolality of the organism internal environment[22]. As a result the osmotic pressures in the extracellular and intracellular liquids of the organism differ sharply and this jump of pressures facilitates transfer of water into the cells leading to the swelling of the latter. At hyponatremia the water

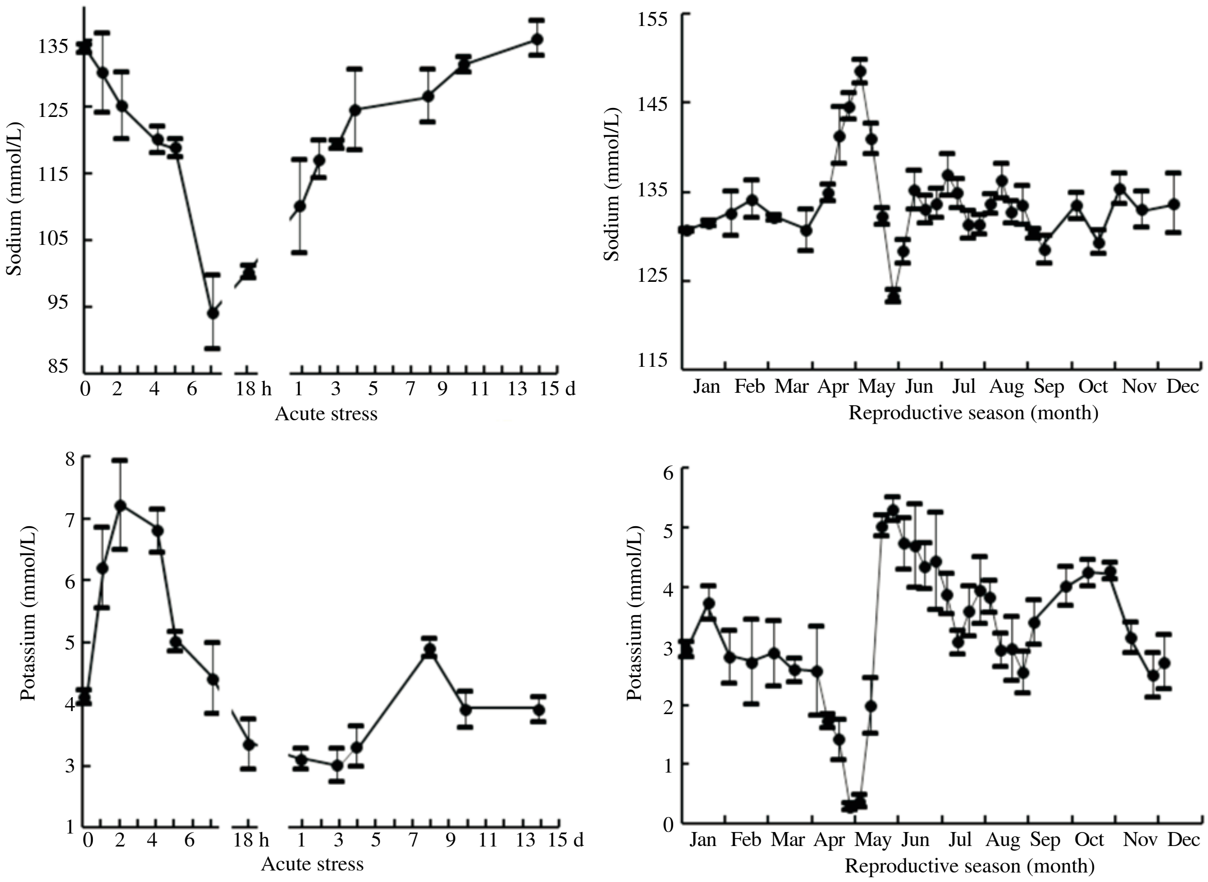

Figure 2. Dynamics of Na, K, concentrations in plasma of the roach at acute stress[16,18], and during different seasons[3,4].

content in the muscles of roach increases by 1.8%[23]. The increase in the water content in brain is especially injurious. The skull prevents expansion of the brain tissue. This is the brain edema at hyponatremia is accompanied by the rise of intracranial pressure with a range of relative negative consequences including high mortality[24].

It was found that during initial two to four hours of stress the leakage of potassium ions from cells prevail resulting in sharp increase in potassium concentration in the blood plasma[16,25] (Figure 2). Considerable increase in the blood plasma potassium content and its decrease in the cells lead to the decline in the gradient of this cation between tissue cells and intracellular liquid. This results in the drop of the membrane potential of cells. The membrane potential is a source of physical energy used for varies functions of cells including secondary transport of a range of substances via surfaces of cellular membranes[26]. Its decrease at stress should lead to the decrease in the ability to fulfill transport functions. Many enzymes are situated on the cellular membranes at their activities depend on the value of cell membrane potential. It was revealed that during the initial stage of stress in common carp the level of potassium in the extracellular liquid increases[27]. This should result in the decrease in the membrane potential and is accompanied by inhibition of acetylcholine esterase activity.

To withstand damaging processes at stress (Figure 1, right part) the protective functions are enhanced by nervous and endocrine systems. These functions relate to the GAS (Figure 1, left part).

2.2. Protective functions at stress

The stressors perceived by nervous system serve as "alarm signals" entering various sectors of brain and hypothalamus. Hypothalamus modifies and coordinates the perceived information and affects the organism via various neuroendocrine pathways.

2.2.1. Hypothalamic-sympathetic-chromaffin cell axis

The first pathway relates to the release of catecholamines from the chromaffin cells, mainly via the preganglion cholinergic filaments of the sympathetic nervous system. However, the transection of these nerves does not prevent fully the secretion of catecholamines during the stress. It is suggested that in fish other factors (*e.g.* transported by the blood) participate in the above mentioned process[28]. Activation of chromaffin system at stress[29,30] leads to fast and sharp (by tenths times) concentration of catecholamines in blood plasma [28,30-34]. These hormones are responsible for various functions. They accelerate the consumption of oxygen by gill by means of increase in the rate of respiration, gill blood current, diffusion capacity of gill and transporting capacity of blood for oxygen via β-adrenergic receptors[28].

Catecholamines enhance the energetic metabolism. These hormones cause disintegration of polymers to monomers owing to increase in glycogenolysis, lipolysis and gluconeogenesis[35-38]. In addition, these hormones enhance oxidative function of mitochondria, functioning of the respiratory chain, oxygen consumption and, as a result, the generation of energy in a form of ATP[39].

2.2.2. Hypothalamic-pituitary-interrenal axis

The second pathway of the realization of protective processes at stress relates to the hypothalamic-pituitary-interrenal axis typical for terrestrial vertebrates and fish[40,41]. Hypothalamus secretes corticotrophin-releasing factor, arginine-vasotocin, isotocin and neuropeptide Y at stress. These substances reach hypophysis and stimulate releasing of adrenocorticotrophic hormone, melanophor-stimulating hormone (MSH) and beta-endorphin[42-44] (Figure 1, left part). As a result, the concentration of these hormones in the blood plasma increases[45-47]. The blood current delivers these hormones into the interrenal tissues enhancing the activity of the latter[29], and increase in the concentrations of cortisol[48-53], and corticosterone in the blood plasma[54].

Cortisol is the main glucocorticoid hormone in fish. It provides various functions: inhibits synthesis of proteins and enhances their degradation in the lymphoid, connective and muscle tissues. The amino acids released from proteins metabolize fast resulting in the negative nitrogen balance. These catabolic processes are determined by the induction of enzymes, especially of the enzymes responsible for catabolism of amino acids and for gluconeogenesis[39,55,56]. As a result, the synthesis of proteins is suppressed which leads to the growth rate retardation. In addition, cortisol stimulates metabolism of lipids by decomposition of fat. As a result, the level in fatty acids increases in the blood plasma[57,58]. Treatment of cortisol leads to the decrease in the level of lipids in the liver and muscles of coho salmon[57].

The reactions related to the energetic metabolism include the antioxidant system. The action of this system is directed towards the neutralization of the free radical processes[8]. The activation of energetic metabolism at stress is "automatically" accompanied by the enhancement of the antioxidant function. Catecholamines and corticosteroids stimulate the energetic metabolism and enhance the antioxidant system.

It is known that during the initial stage of stress the resistance of the organism decrease (the "alarm reaction")[59]. This indicates that at that time the effects of damage and malfunctions prevail over the adaptive reactions. It is suggests that at stress high levels of circulating catecholamines and corticosteroids in the blood plasma cause various disorders, including hyperhydration, loss of electrolytes and nonelectrolytes[32,33,41,60-62] as well as decrease in the resistance of erythrocytes to the blood current[63] in the freshwater fish. It is likely that this opinion is based upon the formal correlation between the increase in the concentrations of various hormones in the blood plasma and simultaneous manifestation of the damaging processes noted at stress. However, in reality the situation is different. Hypophysectomy[64], interrenalectomy and stanniusectomy[65] carried out separately and resulted in the desalination of the fish in the freshwater. The same phenomena are registered at the initial stage of stress in the intact animals resembling the situation when the endocrine glands do not function or excise. The situation is paradoxical: on the one hand at stress the functions of endocrine systems enhance accompanied by the increase in the concentrations of various hormones in the blood plasma, but on the other hand, the disorder of water-salt metabolism takes place at the high functional activity of the endocrine systems (Figure 2) which is typical at the excision of endocrine organs. This phenomenon indicates at the initial stage of acute stress the hormones are seemingly deficient. At the very beginning of the stress response the protective functions related to the GAS (Figure 1, left part) do not compensate for damages (Figure 1, right part). As a result, the latter processes prevail resulting in the decrease of the organism resistance (the "alarm reaction" according to Selye[59]). The protective functions can not withstand development of damaging consequences of the stress instantly. Only with time the adaptive mechanisms repair the damages recovering and stabilizing the organism parameters either at new or at initial levels (Figure 2). This provides an improved stability for an organism (the "stage of resistance" according to Selye[59]). Long and strong stressor causes the exhaustion of the adaptive resources in the organism leading to the prevalence of destabilizing symptoms over the protective reactions (the "stage of exhaustion" according to Selye[59]).

3. Dynamics of physiological-biochemical parameters during the reproduction period in freshwater fish

As at stress the fish during the pre-spawning period exhibit enhancement of protective functions related to GAS (Figure 1, left part). In various fishes shortly before the spawning the activity of hypothalamus hypophysis neurosecretory systems increases which is accompanied by secretion of neurohormones of preoptic-hypophyseal neurosecretory system to blood[1,2]. With blood current the hormones of hypophysis reach interrenal gland[66-69] stimulating release of various corticosteroids into blood[66-71] including cortisol[72-80].

Corticosteroids realize transition of metabolism to the catabolic pathway owing to acceleration of gluconeogenesis, process of formation of glucose from noncarbohydrate sources[55] including protein.Concentration of proteins and amino acids decreases before spawning in fish blood serum and tissues[81-84]. Enhancement of gluconeogenesis and dissipation of glycogen (mainly in the liver) result in the increase blood plasma glucose which takes place before spawning as well[85]. Further the glucose is used for the energetic purposes. In addition, during the pre-spawning period the amount of accumulated fat in the fish body and various organs and tissues sharply decreases[83,86-89]. This indicates the increase in the share of lipolysis in the energetic metabolism.

Before spawning the activation of sympathetic nervous system accompanied by the increase in the blood catecholamine concentrations takes place is fish[90]. Catecholamines acting via β-adrenergic receptors accelerate consumption of oxygen by fish gill increasing the rates of respiration, blood current in gill, diffusion capacity of gill and transporting capacity of blood for oxygen[28].

It was revealed that before spawning the oxygen consumption rise in the whole organism and in separate tissues rises[91,92]. In addition, catecholamines enhance gluconeogenesis[36] and aerobic metabolism by increase in the Kreps cycle substrates[93]. It was also shown that the activity of the enzymes involved in Kreps cycle increases before spawning[94,95] .

As it was shown above during the initial stage of at the development of GAS (Figure 1, left part) the signs of malfunctions of ionic homeostasis were observed (Figure 2). At the pre-spawning period the situation is opposite: at the increase in the manifestations of GAS the protective functions related to maintaining of the ionic homeostasis prevail. For instance, before spawning in the roach blood plasma the concentration of sodium significantly increased by 10.1%; of potassium, decreased by 6.2 times (Figure 2). Pre-spawning increase in the content of sodium was observed in fish species as well[96,97]. This relates to the increase in the concentrations of various hormones in the blood plasma.

It was shown that cortisol enhances uptake of sodium and chlorine ions in the fresh-water fish gill from the environment[65,98]. This hormone facilitates differentiation of chloride cells in gill and increase specific activity of ion-transporting enzymes in gill, intestine and kidney[99,100]. Injections of cortisol and prolactin to hypophysectomized eel *Anguilla anguilla* L. increased concentration of sodium in the blood plasma to normal values and facilitated dehydration of tissues[101]. Adrenalin enhances uptake of sodium by gill[102] and prevents desalination of the organism[103] in the fish adapted to freshwater. The level of prolactin in the fish blood plasma rises before spawning[104]. This hormone decreases elimination of sodium from the organism by decreases in the permeability of gill epithelium and increased reabsorption of this ion in kidney[105].

Before spawning the level of potassium decreases considerably in the blood plasma of roach (Figure 2) and other fish species[97,106,107]. The fish blood plasma potassium level decrease in pre-spawning may relate to a certain extent to the effect of catecholamines. The experiments *in vitro* revealed that these hormones accelerated transport of potassium ions from plasma to erythrocytes of fish[108-112], frogs and pigeons[113]. Considerable decline of potassium level in blood causes increase in the gradient of concentrations of this cation between tissue cells and extracellular fluid. This leads to growth of the membrane potential in the cells. The membrane potential is a source of physical energy used for various functions of cell[26] including increase in the membrane-bound enzymes. For example, considerable increase in the activity of acetylcholine esterase and content of soluble fractions of proteins was revealed in the roach brain before spawning[114]. Increase in the physiological activity of the fish organism before spawning is accompanied by increase in the use of both forms of energy: chemical (ATP) and physical (membrane potential).

Comparative analysis revealed that in the freshwater fish with nonrecurring spawning the protective functions related to GAS enhance both at the initial period of stress and during the pre-spawning period (Figure 1, left part). As for the damaging processes (Figure 1, right part) the pattern of their dynamics during the initial stage of stress is strikingly different: at the initial stage of stress the damaging effects dominate over the protective processes which results in the decrease in the resistance of the organism. As opposite, during the pre-spawning period at the increase in GAS the protective functions are prevailing facilitating increase in the resistance of spawner. It was shown that during the pre-spawning period the resistance to stressors increase[97] along with increase in the thermal resistance in muscles[115] while the concentration of calcium in the erythrocytes and muscle tissues decrease[3,116]. Reduction of the intracellular calcium leads to the stabilization of cytoskeleton[117], determining increase in the resistance to any damaging factors at the level of cell.

The facts given above indicate that during the initial stage of stress due to domination of the damaging effects over the protective reactions the level of resistance of an organism decreases which corresponds to the Selye's "alarm reaction"[59]. Before spawning only protective systems dominate facilitating increase in the level of resistance in the spawner (Selye's "resistance stage"). That is, the absence of the alarm reaction is a characteristic of the pre-spawning period.

Why during the initial stage of stress at the enhancement of adaptive functions (Figure 1, left part) the damaging processes are manifested (Figure 1, right part) while, as opposite, before spawning only protective reactions prevail? This is because the stressors fall upon the organism suddenly enhancing simultaneously both the protective functions and the processes related to the damage of the affected organism. At this situation the protective system activated in the response to stress impact are unable to instantly withstand the damaging effects of extreme factors. As a result, for some time (the durations of this period depends on the strength of the factors and extent of the damage) the damaging processes dominate over the adaptive reactions causing decrease in the organism resistance (the "alarm reaction"). With time, strengthen protective functions eliminate stress-induced malfunctions and provide higher resistance to the organism (the "resistance stage').

As opposite, there are no sudden impacts before the spawning. This is why there are no damages to the organism. The state resembling strong stress occurs in the spawner only at the moment of spawning particularly (Figure 2). Both during the initial stage of stress and during the spawning the content of blood plasma sodium in fish drops sharply while the content of potassium rises. At that, in terms of the strength of the effect the moment of spawning is comparable to the acute stress (Figure 2). This means that during the stress the physiological and biochemical systems of spawner are subject to the strain comparable to that one at the extreme impacts. After the spawning, the resistance of fish decreases[97, 115,118] indicating the exhaustion of the efficiency of protective functions. This state corresponds to the Selye's "stage of exhaustion"[59]. The analysis of the muscles of roach immediately after the spawning confirms the exhaustion of the active physiological systems. During this period the concentration of sodium in the muscles rose by 16.9 mmol/kg wet mass; of potassium, as opposite, decreased by 27.5 mmol/kg wet mass[4]. Presumably, these changes take place owing to insufficient ability (exhaustion) of the sodium pump in the cellular membranes to evacuate the sodium ions in exchange for potassium. Then, within two to three weeks, both at stress and after spawning the parameters of ionic homeostasis recover and stabilize within the normal limits (Figure 2).

This clarifies the biological meaning of the enhancement of protective functions (Figure 1, left part) prior to the beginning of the spawning-induced impact. In the series of generations the acts of spawning repeat in a certain fish species at similar ecological conditions. Such cyclically standard situation promoted a set of adaptations triggering the protective systems in advance to the stress load related to spawning and forming a sort of "safety factor". If before the spawning such safety factor was not developed the reproducing fish may have died either during the spawning or after it owing to sharp decrease in the resistance and in the ability to maintain the ionic homeostasis below the permissible levels. The post-spawning mortality in some less resistant fish is documented[119].

As it was noted above it is believed that during the stress high levels of catecholamines and corticosteroids in the blood plasma cause various malfunctions including impairment of the water-salt homeostasis[32,33,41,60-62,120] in freshwater fish. In this respect the studies on various functions during the pre-spawning period is an ideal model for revealing real effects of neuroendocrine system. During this period the neural and endocrinal functions enhance long before the spawning induced stress. Since before spawning no extreme factor affects the organism there are no damaging effects acting. This is why before spawning the effects of neural and endocrinal systems are manifested per se without simultaneous effects of spawning-related damaging factors.

No damaging processes affect fish during the pre-spawning period. As opposite during this period the protective effects dominate resulting in the increases in the organism resistance. If neuroendocrine systems causes damages to organism as it issupposed by many researchers[32,33,40,41,60-62,120], then the malfunctions should be evident during the pre-spawning period. However it is not occur. Hence, the enhancement of the neural and endocrinal systems during the initial stage of stress and before spawning is directed towards the providing of only the adaptive functions.

4. Conclusions

The comparative analysis revealed that the enhancement of protective functions related to the GAS takes place in the reproducing freshwater fish with nonrecurrent spawning both at the initial stage of stress and during the pre-spawning period. However, during the initial stage of stress the damaging effects dominate over the adaptive processes resulting in the decrease in the organism resistance (the “alarm reaction” according to Selye[59]). As opposite, during the pre-spawning period at the intensification of GAS only the protective systems dominate facilitating the increase in the level of resistance in the spawner (the “stage of resistance” according to Selye[59]). The alarm stage is not manifested before spawning. The state comparable to strong stress occurs in the reproducing fish only at the act of spawning. This is accompanied by decrease in the organism resistance. This indicates the exhaustion of the protective functions and corresponds to the Selye’s “stage of exhaustion”[59]. With time (within two to three weeks), both at stress and after spawning the physiological-biochemical parameters recover and stabilize within the normal limits.

Conflict of interest statement

I declare that I have no conflict of interest.

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